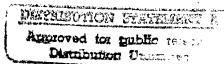
DISPERSAL AND RETENTION OF BENTHIC INVERTEBRATE LARVAE IN FLOWS NEAR A SEAMOUNT

A final report for Grant N00014-89-J-1431 For the period 01 Oct 1988 to 31 May 1996

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SCIENTIFIC OBJECTIVES:

Anecdotal reports of dense aggregations of fish and zooplankton in the water column near seamounts, and of abundant benthic communities on seamount summits have spawned a great deal of speculation over whether seamount-current interactions might be responsible for distinct biological signatures. The general goals of this project were: (1) to investigate effects of mesoscale flows on retention and dispersal of benthic invertebrate larvae near seamounts, and (2) to define the influences of flow-mediated dispersal on population ecology and gene flow in isolated benthic habitats. The primary goal was to test the hypothesis that hydrodynamic features associated with seamounts, such as Taylor Caps, retain larvae and cause them to accumulate near their source. If larval retention occurs on sufficiently long time scales, then we expect larvae to recolonize the source populations, possibly leading to reduced gene flow between adjacent seamounts. A secondary goal of the project (funded as an AASERT Award) was to examine gene flow among seamount populations by characterizing the population genetic structure of seamount-dwelling corals.

Because monitoring larvae in open-ocean waters is a difficult task, a substantial effort was invested in developing and testing techniques for quantifying larvae. These efforts included the use of field and flume experiments to determine larval responses to flow during settlement. These experiments allowed us to infer larval abundance patterns from patterns of colonization on settlement plates.

In the process of pursuing the primary goals of this project, we were also able to investigate related processes, including the response of seamount benthos to an oxygen minimum layer, the effect of seamount-flow interactions on seabirds, and the effect of a three-dimensional flow feature on bivalves in coastal embayments.

APPROACH:

For the primary project, current measurements (analyzed by Ken Brink) and theoretical flow models (developed by Dave Chapman and others) were used to identify regions in the water column near Fieberling Guyot that were likely to retain and accumulate larvae of seamount benthos. Larval abundances in regions with relatively high water residence times were measured

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compared to the theoretical models.

Sequencing of the 16s rRNA region of the mitochondrial DNA of deep-water corals collected on seamounts was used to characterize population genetic structure (and infer gene flow) within and between seamounts on the Northern Hawaiian Ridge. The first (of three) cruises to seamounts near Hawaii has been completed, resulting in collection of > 20 species of corals and other anthozoans. The 16s rRNA region of the mtDNA has been sequenced for all of these species, as well as those collected from Fieberling Guyot and other locations.

SCIENTIFIC RESULTS:

Larval Retention. The distribution patterns of larvae of seamount invertebrates in the plankton and recruits on the settlement panels provide strong evidence for larval retention in seamount flows (Mullineaux, 1994; Mullineaux and Mills, 1997). A surprising result, however, was that larval aggregation occurred on a much larger scale (on the order of a seamount diameter) than initially expected from retention in a classical Taylor Cap. Physical oceanographic studies from Fieberling showed that tidally rectified flows form a large-scale circulation cell that is probably responsible for the observed larval retention. Repeated observations of larval distributions over the seamount showed substantial temporal variation in the abundance and species composition of meroplankton near Fieberling. Reproduction and larval retention in some of these species appeared to be episodic and ephemeral (Mullineaux et al., in prep).

<u>Development of Settlement Plates for Larval Quantification</u>. Flume experiments have been an integral part of our projects, and are critical for developing an ability to use recruitment plates for quantitative analyses of larval abundance and flux in the deep sea. Our initial work on particle contact onto flat plates has allowed us to calculate, at a given larval concentration and flow velocity, how many larvae contact a plate over time (Garland and Mullineaux, 1992). The more difficult problem, however, is how many of those larvae choose to remain and metamorphose. We have answered this question for several species, using barnacle larvae in the flume (Mullineaux and Butman, 1991), and mixed-species assemblages in the field (Mullineaux and Garland, 1993). An understanding of how particles and larvae interact with recruitment plates allows us to use these plates as a tool in our dispersal and recruitment studies in remote habitats, such as vents and seamounts, where frequent sampling with other methods is not feasible. For example, by using flat plates whose leading edges each generated a unique boundary-layer flow, we tested responses of larvae to manipulated flows during a 7-week recruitment experiment on the summit of Cross Seamount. We found that recruitment of deepwater organisms (mostly benthic foraminifers) onto the plates occurred in patterns that could be predicted on the basis of flow alone (Mullineaux and Butman, 1990).

Seamount Coral Phylogeny and Gene Flow. The mitochondrial 16S rRNA of seamount corals shows little variation within species, but significant variation between species. This region of the genome is therefore more appropriate for phylogenetic, rather than population studies. A comparison of the 16S rRNA region among species in the Class Anthozoa showed that members of Orders Antipatharia (black corals) and Ceriantharia (tube anemones) are very dissimilar, and probably should not be grouped together in an independent Subclass (Ceriantipatharia) (France et al., 1995). Further studies of this and other phylogenetic questions, using sequence information from nuclear 18S rRNA and 28S rRNA genes, are currently underway.

Although the mitochondrial 16S rRNA appears not to be a suitable genomic region for population-level studies, nuclear regions, such as internally-transcribed spacers (ITS; occurring between the 18S, 5.8S and 28S rRNA genes) and microsatellites appear to be highly variable within species. Future gene flow studies will concentrate on the genetic variation of ITS regions

and microsatellites in Narella nuttingi, a common, widespread species of seamount coral.

Ecology of Seamount Benthos. An unexpectedly productive sideline to our seamount project was an analysis of current meter data from Cross Seamount, showing that semidiurnal tides were responsible for driving strong currents, often exceeding 20 cm s⁻¹ (Noble and Mullineaux, 1989). While this observation was not surprising in itself, it did lead us to look a year later for internal tides at Volcano 7, a seamount off Mexico that intersects a marked oxygen minimum zone. This study was part of a larger effort that showed that gradients in water column oxygen concentration coincided with vertical distributions of the benthic fauna living on the seamount (Wishner et al., 1990; 1995). Perhaps more exciting was the possibility that internal tides, which displaced the oxygen minimum zone vertically as much as 60 m, were responsible for setting the upper and lower limits for benthic organisms. The vertical distribution of each species would then depend on its tolerances for low oxygen conditions - generating a vertical zonation analogous to a deep-sea intertidal zone.

<u>Seabird Aggregation at Seamounts.</u> An ancillary project to our larval work was a seabird/plankton study conducted by Chris Haney, a postdoc at WHOI. Although anecdotal reports of seabird aggregation at seamounts exist, his study demonstrated for the first time a quantitative difference in the abundance and species composition of birds near Fieberling Guyot relative to open-ocean waters (Haney et al. 1995). The reason for seabird aggregation at Fieberling appeared to be the availability of vertically migrating prey.

Accumulation of Juvenile Bivalves in Coastal Headland Wakes. Circulation generated by interactions between topography and currents influences larval transport processes in coastal as well as deep-water environments. We investigated recruitment processes in topographic flows of coastal environments by quantifying the deposition and aggregation of juvenile bivalves in the secondary flows that form in the wakes of coastal headlands. We demonstrated that these flows aggregate larvae in the water column (Garland and Mullineaux, 1991) and aggregate juveniles on the seafloor (Rankin et al., 1994). Patchiness in bivalve populations appeared to be controlled by the deposition and resuspension of post-larvae, so an understanding of the interactions between behavior of juveniles (e.g., burrowing) and coastal flows will provide new insights into the distribution and dynamics of these shellfish.

SIGNIFICANCE:

The discovery of larval aggregation in seamount-generated flows supports a long-standing hypothesis (that larvae are retained near seamounts) but demonstrates that the mechanism responsible (retention in large-scale tidally-rectified flows) is quite different than initially supposed. The unexpectedly large scale of this retention process has additional implications for larval dispersal between seamounts because the seamounts frequently occur in chains, and are often separated by distances of a seamount diameter or less. Thus, although hydrodynamic retention larvae may prevent larvae from being lost to the open ocean, it may also facilitate larval exchange between closely-spaced seamounts in a chain. This latter question is currently being addressed in our gene-flow studies.

PUBLICATIONS SUPPORTED BY THIS GRANT:

- Mullineaux, L.S. and S.W. Mills. 1997. A test of the larval retention hypothesis in seamount-generated flows. Deep-Sea Research (in press).
- France, S.C., P.E. Rosel, J.W. Agenbroad, L.S. Mullineaux, T.D. Kocher. 1996. DNA sequence variation of mitochondrial large-subunit rRNA provides support for a two subclass organization of the Anthozoa (Cnidaria). Molecular Marine Biology and Biotechnology 5:15-28.
- Haney, J.C., L.R. Haury, L.S. Mullineaux, C.L. Fey. 1995. Seabird aggregation at a deep North Pacific seamount. Marine Biology 123:1-9.
- Wishner, K.F, C.J. Ashjian, C. Gelfman, M.M. Gowing, L. Kann, L.A. Levin, L.S. Mullineaux and J. Saltzman. 1995. The lower interface of the eastern tropical pacific oxygen minimum zone. Deep-Sea Research 42:93-115.
- Mullineaux, L.S. 1994. Implications of mesoscale flows for dispersal and retention of larvae in deep-sea habitats. In: C.M. Young and K.J. Eckelbarger, eds. "Reproduction, larval biology and recruitment of the deep-sea benthos". Columbia University Press, p. 201-222.
- Rankin, K., L.S. Mullineaux and W.R. Geyer. 1994. Transport and deposition of bivalve juveniles in a headland wake. Estuaries 17:655-667.
- Mullineaux, L. S. and E. D. Garland. 1993. Larval recruitment in response to manipulated field flows. Mar. Biol. 116:667-683.
- Garland, E. D. and L. S. Mullineaux. 1992. Particle contact on flat plates in flow: a model for initial larval contact. WHOI Technical Report 92-26.
- Mullineaux, L. S. and C. A. Butman. 1991. Initial contact, exploration, and attachment of barnacle (*Balanus amphitrite*) cyprids settling in flow. Mar. Biol. 110: 93-103.
- Wishner, K., L. Levin, M. Gowing and L. Mullineaux. 1990. Involvement of the oxygen minimum in benthic zonation of a deep seamount. Nature 346: 57-59.
- Mullineaux, L. S. and C. A. Butman. 1990. Recruitment of benthic invertebrates in boundary-layer flows: a deep water experiment on Cross Seamount. Limnol. Oceanogr. 35: 409-423.
- Noble, M. and L. S. Mullineaux. 1989. Internal tidal currents over the summit of Cross Seamount. Deep-Sea Res. 36:1791-1802.

PUBLICATIONS (in preparation):

- Mullineaux, L.S., S.W. Mills, E.D. Garland, I.P. Williams and S. Smith. Temporal variation in water-column distributions of larvae of seamount benthos. Deep-Sea Research.
- Mullineaux, L.S., P.H. Wiebe and S.W. Mills. Dispersal of benthic foraminifers in deep-ocean currents. Journal of Marine Research.
- Mullineaux, L.S., E.D. Garland and R. Signell. Accumulation of bivalve larvae in coastal

headland wakes. Estuaries.

PRESENTATIONS, ABSTRACTS:

- Agenbroad, J.E., S.C. France, L.S. Mullineaux. 1995. Sequence variation in mitochondrial 16S rRNA of three subclasses of anthozoans (Phylum Cnidaria). Poster presented at Keystone Symposium in Santa Fe: Molecular Approaches to Marine Ecology and Evolution.
- Mullineaux, L.S. and S.W. Mills. 1994. Larvae of benthic invertebrates in the plankton around Fieberling Guyot. Trans. Am. Geophys. Un. 75:164.
- Garland, E. D. and L. S. Mullineaux. 1992. Entrainment of late-stage bivalve larvae in coastal eddies. Benthic Ecology Meeting Abstracts.
- Mullineaux, L. S. 1991. Retention of benthic invertebrate larvae in flows near Fieberling Guyot. Sixth Deep-Sea Biology Symposium Programme: 47-48.
- Wishner, K.F., M.M. Gowing, L. Levin and L.S. Mullineaux. 1991. Ecology of a seamount in the oxygen minimum zone in the Eastern Tropical Pacific. Sixth Deep-Sea Biology Symposium Programme: 70-71.
- Mullineaux, L. S. 1989. Vertical transport of benthic invertebrate propagules in flows over Volcano 7 seamount. Trans. Am. Geophys. Un. 71: 155.
- Noble, M. and L. Mullineaux. 1988. Mid-Pacific Internal Tides over Cross Seamount. Trans. Am. Geophys. Un. 69: 1273.

AWARDS, HONORS, ETC.

Promotion to Associate Scientist with Tenure (April 1996)

InterRIDGE Steering Committee - 1995 to present.

NSF LARVE Coordinating Committee - 1995 (LARVE is a 6-year project during 1996-2001 whose objectives are to determine the processes controlling dispersal, gene flow and species distributions of organisms living at hydrothermal vents)

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